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ASSOCIATION OF HOMOLOGOUS CHROMOSOMES IN TETRAPLOID CELLS OF DIPTERA.

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A characteristic feature of chromosome behavior in the Diptera is the paired association of homologous chromosomes[1] in the diploid cells, somatic as well as germinal. This association is particularly striking in the early prophase of each cell generation, when the two homologous chromosomes are closely approximated—so closely, indeed, as to resemble a single element in many cases.[2] Like the association that occurs during synapsis in the germ cells of most organisms, this is apparently the result of an attraction between similar or identical elements in the conjugating chromosomes.

In considering the nature of the attractive force involved here, one of the first questions to arise is whether an equilibrium is established when two homologous chromosomes associate (analogous to a magnetic attraction) or whether the attraction extends to an indefinite number of members, so long as they are homologous. The observations on sporogenesis in certain triploid and tetraploid plants by El. and Em. Marchal ('11), Digby ('12), Osawa ('20), and Belling ('21) indicate that in the metaphase following synapsis homologous chromosomes are frequently grouped together, although not uniformly so. This indicates that there is, sometimes at least, an attraction between homologous chromosomes in numbers greater than two; but it tells little about the detailed nature of the association.

The observations of Holt ('17), of Metz ('16), and of Bridges ('22) on multiple chromosome groups of somatic cells in certain

1 First described by Stevens in 1907 and 1908.

2 See Metz, '16, for a detailed account.

flies[1] have shown that the chromosomes regularly lie in clusters during metaphase, and that each cluster consists of the three, four, or more homologous members.[2] In prophase (Holt, '17; Metz, '16, Figs. 109, 110) the association of homologues is closer than in metaphase. Here again, however, there is some doubt about the exact nature of the association. Holt's observations on *Culex* seem to lead to two different views on this question, without indicating which is correct. According to one view sister chromosomes associate more closely than homologues that are not sisters. Evidence cited on p. 612, for instance, ". . . suggests that a parasynaptic union of sister chromosomes takes place in the telophase. . . ." This is supported also by her Figs. 13, 14, and 15, in which each original pair of chromosomes seems to be represented by two associated bodies, each of which is presumably made up of four or more sister chromosomes. If this is the case, the association between sister elements is closer than that between homologous, non-sister elements. But the statement is also made (p. 613) that "it is believed" that in multiple complexes the chromosomes conjugate "in three groups of homologous individuals" (three being the haploid number in *Culex*). The latter statement implies that there is no distinction between homologous and sister chromosomes.

In the observations of the writer (l.c.) on *Fucellia* no attempt was made to analyze the details of the prophase association or to discriminate between sister and non-sister homologues.

The present paper is concerned with additional evidence on this point. The data are taken from some exceptionally clear prophase figures obtained in tetraploid ovarian cells of *Sarcophaga*.[3]

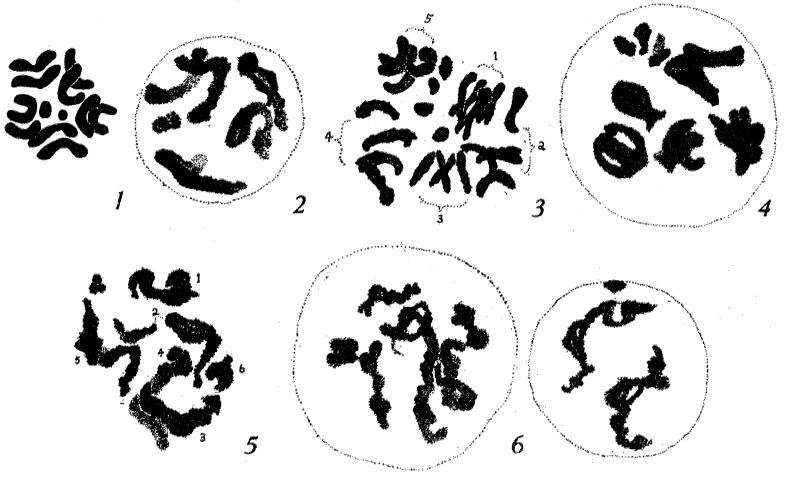
The normal chromosome group of *Sarcophaga* consists of five pairs of long chromosomes and one pair of short (sex) chromosomes. These are represented in Fig. 1, taken from a spermatogonium. In the early prophase, when the association of homo-

[1] Holt's observations were on *Culex;* those of Metz were on *Sarcophaga* and *Fucellia;* those of Bridges were on *Drosophila.*

[2] That the associating chromosomes are homologous cannot be doubted in the light of present cytological and genetical knowledge.

[3] The species has not been identified in this case, but all of my *Sarcophaga* material, including several identified species, shows essentially the same (normal) chromosome group throughout.

logues is intimate, the six pairs resemble six single chromosomes, as shown in Fig. 2 (ovarian cell). The conditions found in tetraploid cells are represented in Figs. 3 to 6. These cells were found scattered about in the somatic tissue of the same ovary from which Fig. 2 is taken. The tetraploid cells are so large that the



EXPLANATION OF FIGURES.*

*I am indebted to Miss Ruth Lincks for making the drawings for the figures.

All figures were drawn to the same scale, with the aid of a camera lucida. Numbers 1 and 2 are from diploid cells; numbers 3 to 6 are from tetraploid cells; numbers 2 to 6 are from the same ovary.

FIG. 1. Typical metaphase (from a spermatogonium) showing the chromosomes loosely associated in pairs. The smallest pair is the sex chromosome pair (XY).

FIG. 2. Typical prophase (ovarian cell) showing the close association of homologous chromosomes.

FIG. 3. Tetraploid chromosome group in metaphase showing loose association in fours instead of twos. The four smallest elements are the sex chromosomes (XXXX).

FIG. 4. Late prophase of a tetraploid nucleus showing close association in fours.

FIGS. 5 AND 6. Early prophases of tetraploid cells showing intimate association of homologous chromosomes.

nucleus and some of the chromosomes are usually cut in sectioning; but a few nuclei have been found entire, or nearly so. One of these, a metaphase, is represented in Fig. 3. This figure brings out the loose association of chromosomes, characteristic of the

metaphase. Fig. 4 shows the closer association of late prophase. The intimate association of the early prophase is represented in Figs. 5 and 6. In the former each of the long bodies (numbered 1, 2, 3, 4, 5) is composed of four thread-like chromosomes, closely approximated side by side. This nucleus is almost entire, but the body numbered 2 appears to be cut at the point where the number is placed. Number 6 is presumably the set of small sex chromosomes. Fig. 6 represents a slightly earlier prophase in which the threads are somewhat more attenuated. The nucleus here is cut and lies in two sections, so that only three or four of the long, tetravalent bodies are complete. These show the same intimate association of homologous threads, however, as do the similar ones in Fig. 5. In both of these figures and in other prophases of a corresponding stage the association of homologues is so close that the individual threads can only be distinguished here and there.

As the figures indicate, the four threads of each body in the early prophase appear to be associated in equal degree. I can find no indication of a closer association of sister elements than of non-sister elements within the tetrad.

It appears, then, that in these cases the force which brings homologous chromosomes together is exerted equally between the respective members when four are present.[1] This agrees with the observations of Holt on *Culex* if we accept the latter of the two views suggested above—that the chromosomes conjugate in three groups of homologous individuals, without any distinction between sister and non-sister homologues.

Possibly this equivalence of association applies only to the gross relationships and does not represent the actual interrelations beyond the limits of visibility. That is a question, however, which can hardly be answered by a study of somatic cells. In the case of synapsis in the germ cells it may be possible to answer it by

[1] The question might be raised here as to whether these chromosomes actually come together, or whether they owe their association to successive divisions of the orginal prophase chromosomes *in situ*. The latter view involves the assumption that such cells do not multiply, and that each case represents an independent origin from a diploid cell. The evidence is against such an assumption, for all stages of division (prophase, metaphase, anaphase, etc.) may be found in these cells, and in some pieces of tissue nearly all of the cells are of the same multiple chromosome type (*e.g.*, in *Fucellia*).

means of genetical studies on "crossing over" in tetraploid or other multiple chromosome races.

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